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A trait database for marine copepods

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Abstract. The trait-based approach is gaining increasing popularity in marine plankton ecology but the field urgently needs more and easier accessible trait data to advance. We compiled trait information on marine pelagic copepods, a major group of zooplankton, from the published literature and from experts and organized the data into a structured database. We collected 9306 records for 14 functional traits. Particular attention was given to body size, feeding mode, egg size, spawning strategy, respiration rate, and myelination (presence of nerve sheathing). Most records were reported at the species level, but some phylogenetically conserved traits, such as myelination, were reported at higher taxonomic levels, allowing the entire diversity of around 10 800 recognized marine copepod species to be covered with a few records. Aside from myelination, data coverage was highest for spawning strategy and body size, while information was more limited for quantitative traits related to reproduction and physiology. The database may be used to investigate relationships between traits, to produce trait biogeographies, or to inform and validate trait-based marine ecosystem models. The data can be downloaded from PANGAEA, doi:10.1594/PANGAEA.862968.

1 Introduction

The trait-based approach is an increasingly popular framework in ecology that aims to describe the structure and function of communities or ecosystems in a simple way. It seeks to identify the main characteristics of organisms that control their fitness (Litchman et al., 2013). Organisms must be successful in three main missions in order to thrive: feeding, survival, and reproduction. Functional traits determine the outcome of one or several of those missions.

Functional traits are generally understood as heritable properties of the individual that are interrelated through trade-offs and selected by the environment. Furthermore, a criterion of measurability appears useful: traits should be measurable on the individual without any assisting information (Violle et al., 2007). We therefore consider, for example, “feeding mode” to be a functional trait, but not “preferred habitat”, as it depends on the characterization of the environment in which an individual occurs.

The trait-based approach has been of great value in plant ecology. Studying the spatiotemporal variation of traits in plant communities has permitted insights into community

emergence and ecosystem functions beyond the limits of approaches purely based on taxonomic diversity (van Bodegom et al., 2014; Violle et al., 2014; Westoby et al., 2002). The trait-based approach therefore not only advanced plant ecology, but also facilitated the description of key ecosystem processes like carbon uptake and storage, and thus continues to push related fields like biogeochemistry and climate science forward.

More recently, the trait-based approach has been adopted in marine plankton ecology (Barton et al., 2013; Litchman and Klausmeier, 2008; Litchman et al., 2013). One key group of marine zooplankton, for which traits and trade-offs are relatively well understood, is copepods (Kiørboe, 2011). These ubiquitous crustaceans typically dominate the biomass of zooplankton communities (Verity and Smetacek, 1996), play a central role in marine food webs, and affect the global carbon cycle (Jónasdóttir et al., 2015).

We focus here on a set of 14 commonly described functional traits for marine copepods, for which data are available (Fig. 1). The set includes one trait affecting all life missions, three feeding-related, six growth-related, and three

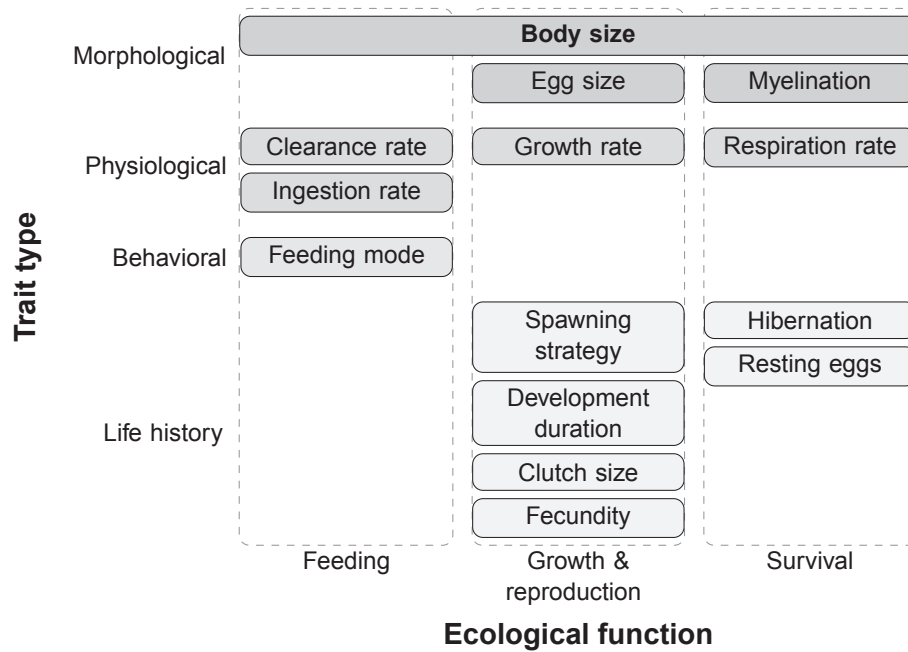


Figure 1. Copepod traits included in the database, arranged according to the framework of Litchman et al. (2013). The vertical axis groups traits by trait type and the horizontal axis by ecological function. Body size (bold) transcends several functions.

reproduction-related traits. Body size affects all life missions since it is related to several essential properties including metabolism, feeding, growth, mortality, mobility, and prey size (Litchman et al., 2013). Feeding-related traits include clearance rate, i.e., the effective volume of water cleared for prey items per unit of time when the prey concentration is low (Kjørboe and Hirst, 2014); maximum ingestion rate – the feeding rate at non-limiting food concentration (Kjørboe and Hirst, 2014); and feeding mode (behavior) (Kjørboe, 2011). For the latter, the following behaviors are separated: ambush-feeding copepods remain largely immobile and wait for approaching prey; cruise-feeding copepods move actively through the water in search of prey; feeding-current feeders produce a current by beating their appendages and capture entrapped prey; particle-feeding copepods colonize large aggregates of marine snow on which they feed for extended periods; and parasites colonize larger hosts, such as fish, from which they feed. Growth-related traits include maximum growth rate (the maximum amount of body mass gained per unit time) and development duration at non-limiting food availability. Reproductive traits include spawning strategy, which distinguishes between free spawners that release their eggs into the water, and sac spawners that carry their eggs until hatching; egg size; clutch size (eggs produced in one “spawning event”), and fecundity (the number of eggs produced over the life-time of a female). Finally, the traits related to survival are myelination (the insulation of nerve tracts with membranous tissue, which greatly enhances the speed of signal transmission and allows rapid response to predators; Lenz et al., 2000); respiration rate, the volume of

oxygen consumed per unit time; hibernation, which allows individuals to endure adverse conditions over seasonal time frames; and resting eggs, which can endure adverse conditions over several decades (Williams-Howze, 1997).

Here, we followed a recent call for efforts to collect trait data for plankton (Barton et al., 2013) and established a database for the 14 copepod traits introduced above. We screened the literature for information on marine copepods, mainly pelagic taxa. Particular attention was given to the trait body size, feeding mode, egg size, spawning strategy, myelination, and respiration rate, for some of which we have examined the biogeography elsewhere (Brun et al., 2016a). We present data coverage as well as trait distributions for the most important pelagic copepod families and discuss data collection methods as well as limitations. The data can be found on PANGAEA: doi:10.1594/PANGAEA.862968 (Brun et al., 2016b).

2 Data

2.1 Origin of data

Our data consist primarily of material from previous data compilations on individual traits, complemented by information from the primary literature and expert judgements. In total 91 references were consulted, with a few sources contributing the majority of the data (Table 1). The primary literature was screened mainly for information on the focal traits of body size, feeding mode, egg size, spawning strategy, and respiration rate. For feeding mode, we also used ex-

pert judgement: feeding modes have been described in the literature only for a minor fraction of copepod species. Where no information on feeding mode was available, we studied the morphology of the feeding appendages and, if feasible, grouped the taxa into two categories of feeding activity (active versus passive feeding, see Sect. 2.2.1).

2.2 Trait information

Aside from the ecological categorization shown in Fig. 1, the traits considered may be separated as categorical–qualitative traits and continuous–quantitative traits, which involve different methods of data storage.

2.2.1 Qualitative traits

Here, qualitative traits include feeding mode, spawning strategy, myelination, hibernation, and resting eggs. We treat qualitative traits as unique either on the species level or on higher-order taxonomic levels. For hibernation and resting eggs, we report records on the species level, including information about the observed life stage in the case of hibernation. Species for which hibernation and resting egg production have been observed may be considered as having the potential to express the trait, without necessarily expressing it in every individual.

Feeding mode, spawning strategy, and myelination were assumed to be conserved in the taxonomy, yet we are aware that this is not always the case (Sect. 4.2). Records are therefore also reported for genera, families, and orders, assuming that all species from the corresponding taxonomic branch carry the trait. We distinguish five not-necessarily exclusive feeding modes, i.e., ambush feeding, particle feeding, feeding-current feeding, cruise feeding, and parasitic feeding (Kiørboe, 2011). Feeding modes are further clustered into different feeding activity levels (Table 2). Spawning strategy distinguishes between free spawner and sac spawner that may be separated further into single egg sac, double egg sac, or egg mass. Finally, myelination distinguishes between myelinated and unmyelinated taxa.

Not all information on feeding mode and spawning strategy was reported with the same degree of confidence. We therefore added a “confidence level” column for these traits, which classified the records on a scale ranging from 1 (high confidence) to 3 (low confidence).

2.3 Quantitative traits

Quantitative traits include three size traits, four physiological rate traits, fecundity, and development duration. Where possible, we report mean, minimum, and maximum trait value as well as standard deviation and sample size for each record. Quantitative traits were collected mainly for adults, but where available we also include information on juvenile life stages. Several records may exist for each species,

sex, and life stage, originating from different measurements or references. In some cases quantitative traits are reported on taxonomic levels higher than species. This is usually due to limited taxonomic resolution, and therefore such records should not be assumed to represent the entire taxonomic branch. For each quantitative trait, we defined standard units in which the data are reported (summarized in the “explanations” tab in the data tables). Where conversions were not straight forward, we report different types of trait measurements, e.g., we distinguish between total length and pro-some length for body size and between outer diameter and μg carbon for egg size. The taxonomic overview of quantitative traits shown below is based on species-wise averages of the data, restricted to adult individuals, where life-stage matters.

2.4 Meta-information

2.4.1 Taxonomy

Around 10 800 marine copepod species are currently recognized (Walter and Boxshall, 2016). Taxonomic classification of these small crustaceans is not trivial and has changed considerably over the past century. In order to ensure consistency, all the taxa reported were updated based on the latest (2 June 2016) (re)classification by Walter and Boxshall (2016) with the finest possible resolution on the species level. We also added the full taxonomy of marine copepods to our data tables in order to allow easy translation of the records to the desired taxonomic level. However, we encourage readers to use the online version on www.marinespecies.org/copepoda instead to ensure that the information used is up to date. For simplicity, we restrict the data presentation in this paper to a subset of the taxonomy, mainly containing families with important pelagic species (Appendix A).

2.4.2 Life-form

Copepods undergo a complex life cycle, including an egg stage, six naupliar stages, and six copepodite stages that may show distinct traits. Furthermore, distinct differences between sexes are possible, for example, through sexual size-dimorphism (Hirst and Kiørboe, 2014). If necessary, we therefore included information about life stage and sex of an individual in a “life form” column (Table 3). Some authors distinguish between sexes already in copepodite stages IV and V (e.g., Conway, 2006). We disregard this separation to optimize consistency among the different sources.

2.4.3 Location

Traits can vary considerably as a function of the geographical location, in particular if they are observed on organisms in the field. Information about the geographical location, however, is not readily available in traditional data compilations.

Table 1. Important references used in the database and their taxonomic and geographical foci; a full list of references is given in the data tables.

Reference	Trait(s)	Focal taxa	Focal region
Benedetti et al. (2015)	Feeding mode	Abundant copepods	Mediterranean Sea
Boxshall and Halsey (2004)	Spawning strategy	Calanoida	Global
Conway et al. (2003)	Body size	Copepods	Southwestern Indian Ocean
Conway (2006)	Body size	Common planktonic copepods	North Atlantic
Conway (2012)	Body size, spawning strategy	Copepods	Southern Britain
Hirst and Kiørboe (2014)	Body size	Copepods	Global
Ikeda et al. (2007)	Respiration rate	Marine pelagic copepods	Global
Kiørboe and Hirst (2014)	Clearance rate, ingestion rate, growth rate, respiration rate	Marine pelagic copepods	Global
Lenz (2012)	Myelination	Calanoida	Global
Mauchline (1998)	Egg size, clutch size, fecundity, hibernation, resting eggs, generations	Calanoida	Global
Neuheimer et al. (2016)	Egg size	Copepods	Global
Razouls et al. (2005–2016)	Body size	Marine planktonic copepods	Global
Walter and Boxshall (2016)	Taxonomy	Copepods	Global

Table 2. Feeding modes included in the database and their categorization by feeding activity.

Feeding activity	Feeding modes
Passive	Ambush feeding, particle feeding
Active	Feeding currents, cruise feeding
Mixed	Combination of active and passive modes
Other	Parasitic

Nevertheless, we reported information about location where it was available.

2.4.4 Other

Further meta-information includes temperature, body mass, and general comments. Physiological rate traits (growth rate, respiration rate, clearance rate, and ingestion rate) depend on both body mass and temperature (Kiørboe and Hirst, 2014), which we also report for records of these traits. For body mass, we further distinguish dry mass or carbon mass. Further relevant meta-information may be provided in the “comment” field.

2.5 Data conversions

We consider our database to be primarily a source of information, and we generally leave it to the user to select methods and assumptions for aggregation and conversions. Nevertheless, we made some conversions for physiological rate traits and egg size in order to facilitate their comparability. Physiological rate traits largely stem from Kiørboe and Hirst (2014), who converted traits to carbon-specific values and to a standard temperature of 15 °C. For growth rate, clearance rate, and ingestion rate, we included these converted values,

while we recalculated them for respiration rate. Furthermore, we calculated development rate at 15 °C based on inverted estimates for development duration. Temperature corrections were performed assuming a Q_{10} value of 2.8 (Kiørboe and Hirst, 2014). The Q_{10} value is the factor by which physiological rates increase when temperature is increased by 10 °C. To estimate respiration rates we also needed information on carbon content, which we derived by converting weight information using the empirical relationships provided in Kiørboe (2013). Egg size was reported in part as carbon content. For comparability, we also report conversions of these values to outer diameters assuming a spherical egg shape and a carbon density of $0.14 \times 10^{-6} \mu\text{g C } \mu\text{m}^{-3}$ (Kiørboe and Sabatini, 1995).

3 Results

3.1 Data coverage

In total, the data tables include 9306 records for the 14 traits investigated. With 7131 records, the most information was available for body size by far (Fig. 2). However, for taxonomically clustered traits like myelination, only a few records were necessary to cover all marine copepods. Similarly, relatively few records were available for hibernation and resting eggs, but they likely cover the existing information in the literature and therefore the dominant species expressing these traits. For quantitative traits related to reproduction and physiology, information was generally more limited. Among taxa, the best data coverage was available for the order Calanoida. However, some non-calanoid families also showed relatively high data coverage, including Oithonidae and Oncaeidae. For non-pelagic copepods, information was mainly available on myelination and – for Siphonostomatoida – on feeding mode.

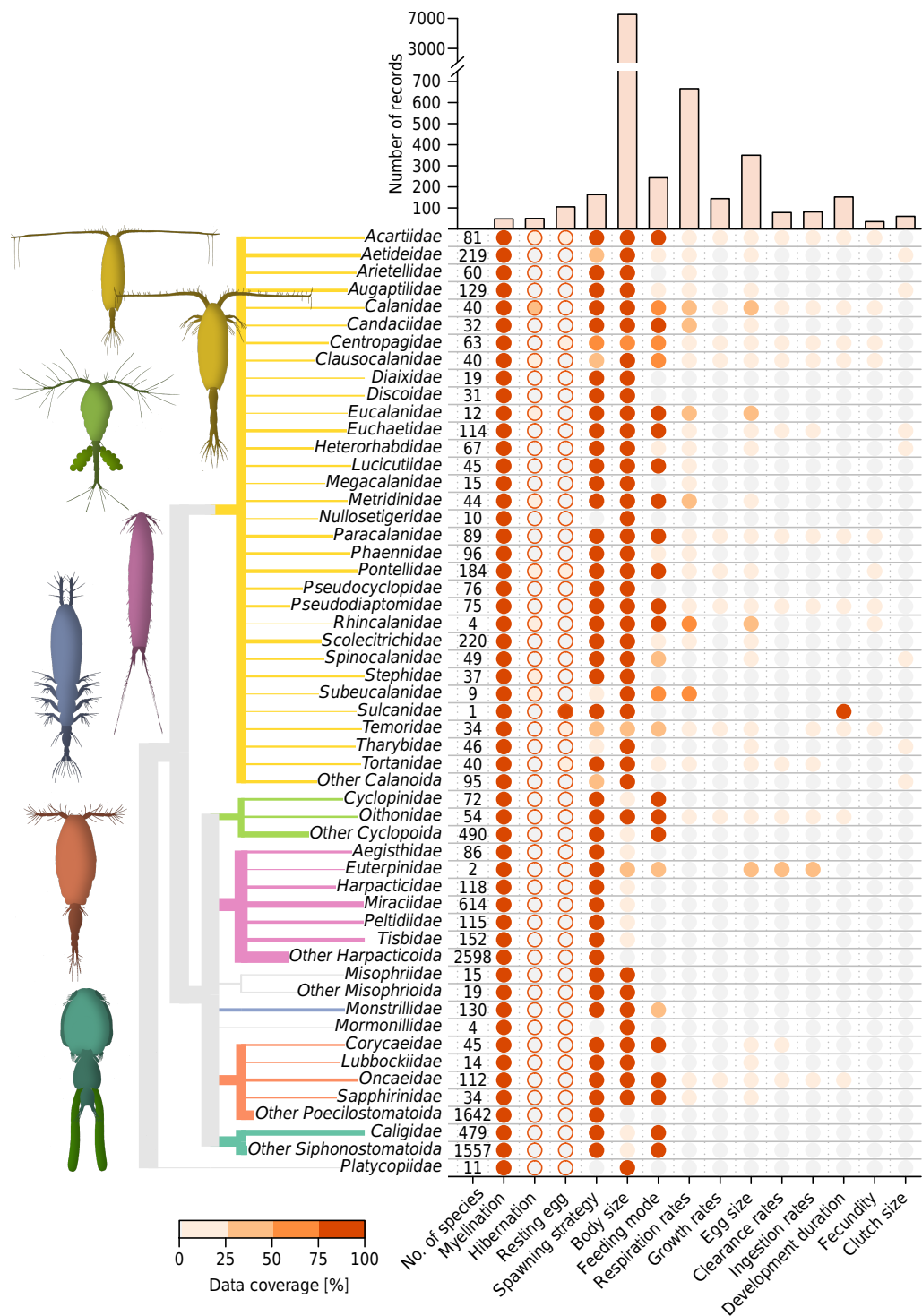


Figure 2. Trait-wise data coverage for taxonomic families of marine copepods. The top shows the number of database records per trait. The left shows the taxonomic tree of important families weighted by number of species, including illustrations of type species for the dominant orders. Illustrated species are (from top to bottom) *Calanus finmarchicus*, *Metridia longa*, *Oithona nana*, *Microsetella norvegica*, *Monstrilla helgolandica*, *Oncaea borealis*, and *Caligus elongatus*, representing orders according to their color code; right shows the table indicating the fraction of species for which data were collected per family and trait. Note that since some traits are taxonomically clustered, a few records for higher-order taxa may suffice to describe the entire diversity. Orange rings indicate traits for which we likely covered the vast majority of trait-carrying species that have been reported in the literature (hibernation and resting eggs). Although we only report a few species, they likely contain most of the existing biomass showing the trait. However, future discoveries may expand this list.

Table 3. Abbreviations used for the classifications of life stage and sex in the database.

Abbreviation	Definition
NI, NII, NIII, NIV, NV	Naupliar stages 1–5
N	Nauplius, no information about stage
CI, CII, CIII, CIV, CV	Copepodite stages 1–5
C	Copepodite, no information about stage
A	Adult (copepodite stage 6), no information about sex
F	Adult female
M	Adult male

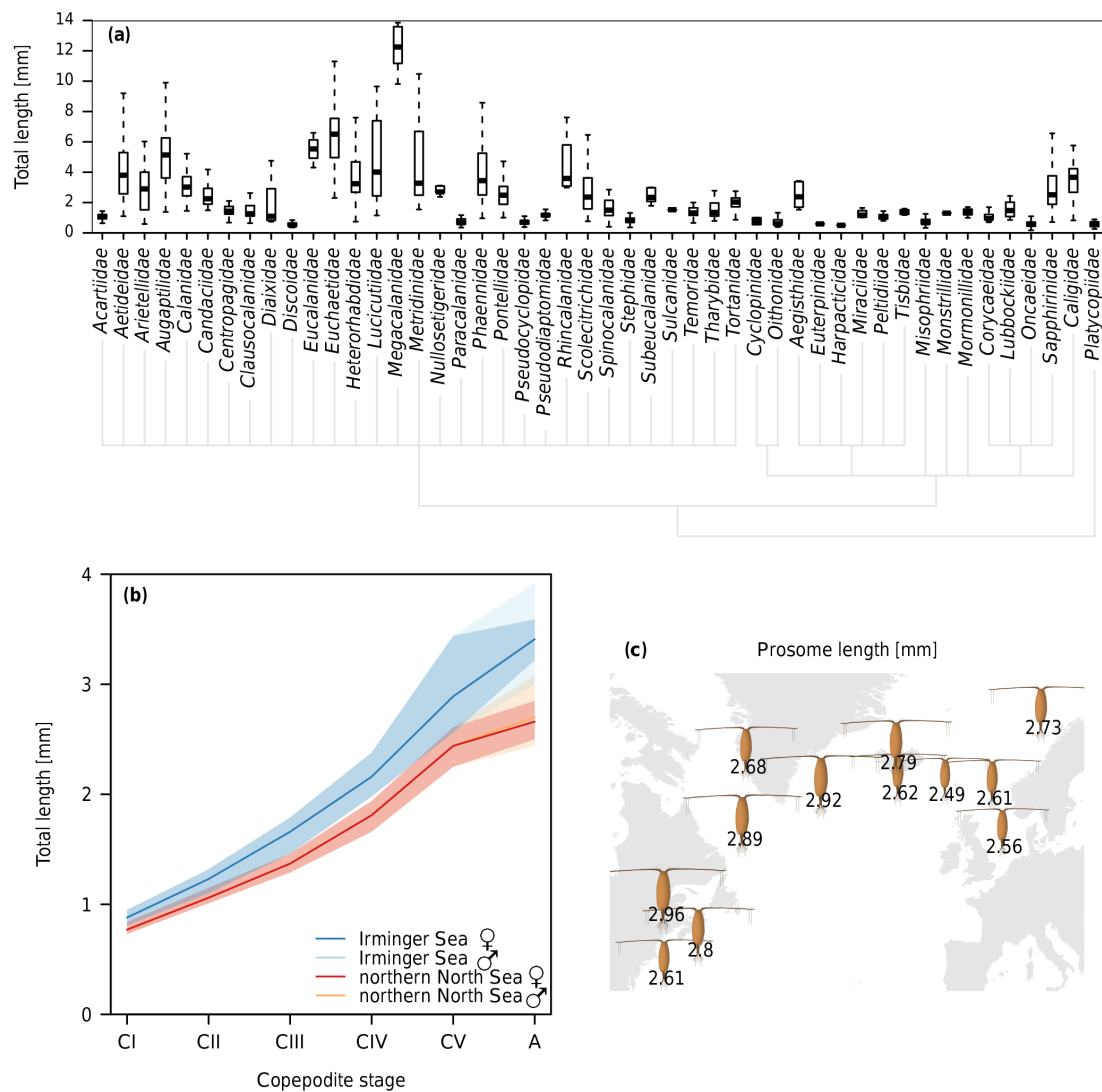


Figure 3. Variation of body size in marine copepods as a function of taxonomy, life stage, and location. Panel (a) shows box plots of total body length for the most important families covered. Thick lines on box plots illustrate median, boxes represent the interquartile ranges, and whiskers encompass the 95 % confidence intervals. Total length of *Calanus finmarchicus* as a function of copepodite stage in two different areas is shown in panel (b). For males and females mean values are shown as solid lines and mean \pm standard deviation are shown as transparent polygons. Distribution of female prosome length of *C. finmarchicus* in the North Atlantic is shown in panel (c).

3.2 Body length

Total body length varies between 0.095 mm for *Acartia ba-corehuiensis* and 17.4 mm for *Bathycalanus sverdrupi*, and body size is largest on average for calanoid copepods. Our data indicate shortest body lengths for the harpacticoid families Harpacticidae, Discoidae, and Euterpinae, as well as for Oithonidae and Oncaeidae, with median total lengths of adults between 0.5 and 0.6 mm (Fig. 3a). Families with the largest species are Megacalanidae followed by Euchaetidae and Eucalanidae, with median adult body lengths of 12.25, 6.51, and 5.54 mm, respectively. The highest interquartile range of body lengths is found for Lucicutiidae with 4.57 mm.

Body size does not only vary between species but also within them. Not surprisingly, body size increases considerably throughout the ontogeny of copepods (Fig. 3b). However, significant variations in body size are also observed as a function of the geographic location. When compared in space, the average prosome lengths of adult females of *C. finmarchicus* vary between about 2.5 and 3 mm across the North Atlantic, corresponding to a mass difference of a factor of over 1.7 (Fig. 3c).

3.3 Egg size

Egg diameter varies between 37.3 μm for *Oncaea media* and 870 μm for *Paraeuchaeta hansenii*. The non-calanoid families covered (Oncaeidae, Corycaidae, Oithonidae, and Euterpinae) tend to have smaller eggs than the calanoid families (Fig. 6a). With a median diameter of 51.5 μm , Oncaeidae is the family with the smallest egg sizes, while Augaptilidae have the largest eggs with a median diameter of 554.3 μm . The highest diversity of egg diameters is found for Euchaetidae with an interquartile range of 365.5 μm .

3.4 Myelination

Myelination only occurs in calanoid copepods and is assumed to be either consistently present or absent within families. Major families with myelinated axons are Aetideidae, Calanidae, Euchaetidae, Paracalanidae, Phaennidae, and Scolecitrichidae (Fig. 7a).

3.5 Clearance rate

For adult copepods, carbon-specific clearance rate corrected to 15 °C varies between 224 $\text{mL h}^{-1} \text{mg C}^{-1}$ for *Calanus pacificus* and 3067 $\text{mL h}^{-1} \text{mg C}^{-1}$ for *Oithona nana*. On the family level, Calanidae show the lowest corrected clearance rates, whereas the highest rates are found for Acartiidae (Fig. 4a). The number of data points for adult copepods is only 18 for clearance rate, as life stage information is missing for most records (Fig. 4b).

3.6 Ingestion rate

Carbon-specific ingestion rate at 15 °C ranges between 15 $\mu\text{g C h}^{-1} \text{mg C}^{-1}$ for *Calanus pacificus* and 116 $\mu\text{g C h}^{-1} \text{mg C}^{-1}$ for *Euterpina acutifrons*, when comparing adult individuals. On the family level, the lowest ingestion rates are found for Tortanidae, and the highest values are found for Euterpinae (Fig. 4c). Again, only 21 data points are available for ingestion rates of adult copepods, as life stage information was missing for most records (Fig. 4d).

3.7 Growth rate

Specific growth rate at 15 °C varies between 5 $\mu\text{g C h}^{-1} \text{mg C}^{-1}$ for *Labidocera euchaeta* and 19 $\mu\text{g C h}^{-1} \text{mg C}^{-1}$ for *Calanus finmarchicus*. In accordance, the families of these taxa, Pontellidae and Calanidae, have, respectively, the lowest and highest specific growth rates among all families for which we have data (Fig. 4e). For Calanidae, the group for which most information was available, we found the highest diversity of growth rates, with an interquartile range of 10 $\mu\text{g C h}^{-1} \text{mg C}^{-1}$.

3.8 Respiration rate

Specific respiration rate at reference temperature is lowest for *Hemirhabdus grimaldii* at 0.3 $\mu\text{L O}_2 \text{ h}^{-1} \text{mg C}^{-1}$ and highest for *Acartia spinicauda* at 53.8 $\mu\text{L O}_2 \text{ h}^{-1} \text{mg C}^{-1}$. Among families, respiration rates are lowest for Heterorhabdidae (median = 0.7 $\mu\text{L O}_2 \text{ h}^{-1} \text{mg C}^{-1}$) and highest for Sapphirinidae (median = 25.0 $\mu\text{L O}_2 \text{ h}^{-1} \text{mg C}^{-1}$) (Fig. 4f). The highest interquartile range of specific respiration rates is found for Acartiidae. Most of the records on respiration rates contain life stage information and are made for adult individuals (Fig. 4g).

3.9 Feeding mode

Feeding modes differ among taxonomic orders (Fig. 5). Calanoid copepods are active feeders and in some cases mixed feeders (Acartiidae and Centropagidae). Active feeding is also seen in the order Monstrilloida and in the family Oncaeidae of the order Poecilostomatoida. Passive feeding prevails in the orders Cyclopoida and some families of the order Harpacticoida, as well as in the family Corycaidae of the order Poecilostomatoida. Parasitic copepods are found in the order Siphonostomatoida and in the family Sapphirinidae of the order Poecilostomatoida.

3.10 Development rate

Development rate through copepodite stages corrected to 15 °C varied between 0.04 d^{-1} for *Sulcanus conflictus* and 0.17 d^{-1} for *Eurytemora affinis*. On the family level,

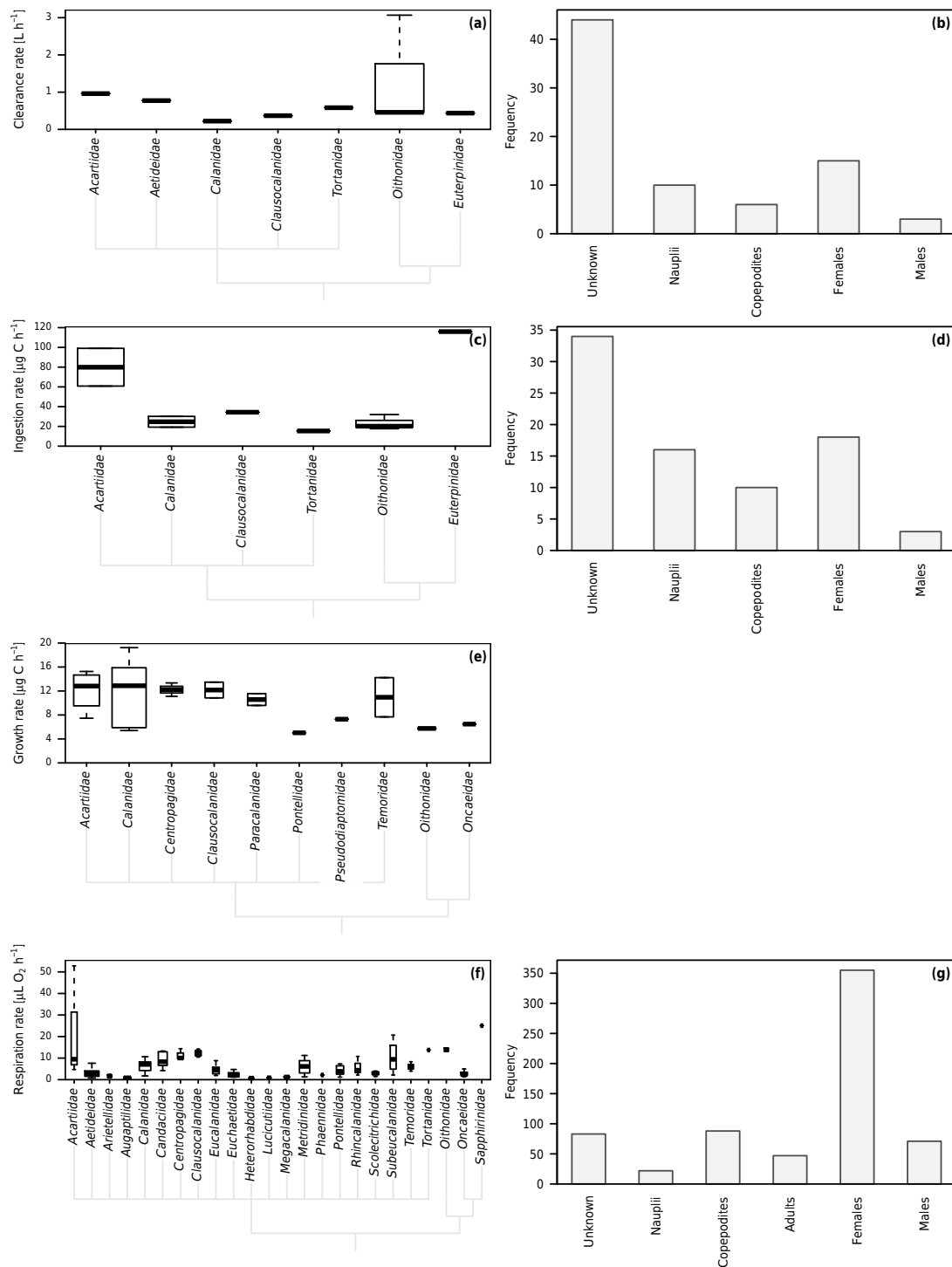


Figure 4. Physiological traits of adult copepods grouped by family, and frequency of life stage information available for the records. Family-wise box plots for clearance rate (a), ingestion rate (c), growth rate (e), and respiration rate (f). Illustrated rate values are per milligram carbon and corrected to 15 °C. Thick lines on box plots illustrate median, boxes represent the interquartile ranges, and whiskers encompass the 95 % confidence intervals. Box plot width is proportional to the square root of sample size. Bar plots in panels on the right (b, d, g) indicate frequency distribution of life stage levels for the traits reported.

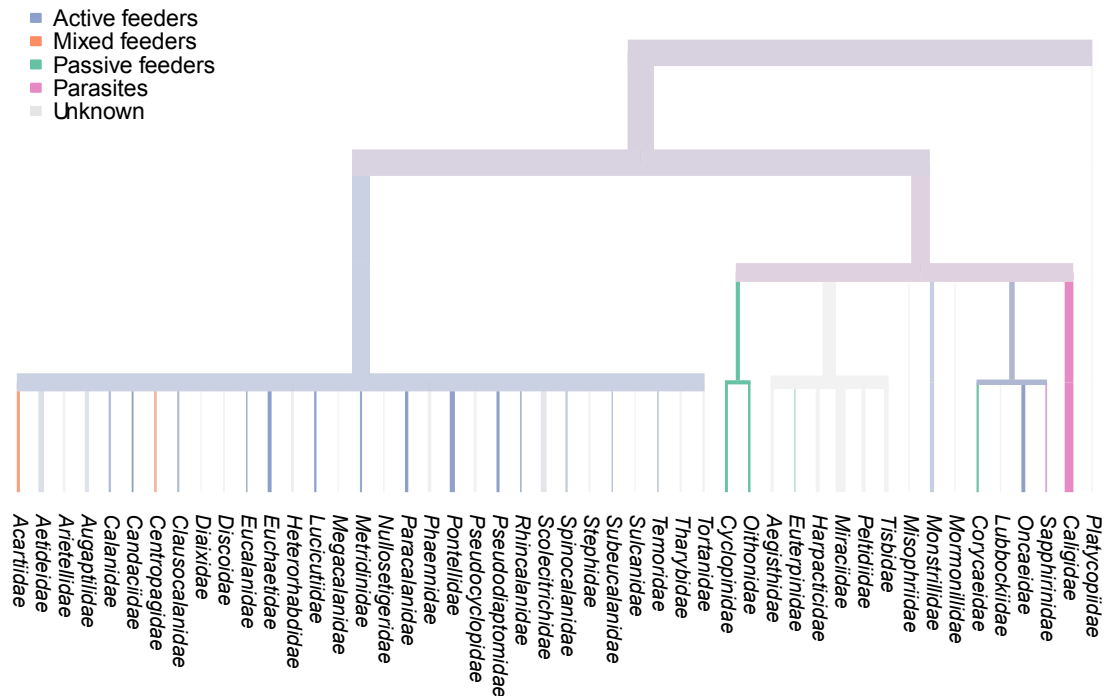


Figure 5. Taxonomic distribution of feeding modes in the most important families of marine planktonic copepods. Distinguished are active feeders (blue), mixed feeders (orange), passive feeders (green), and parasites (pink). Taxa for which no information was available are shown in grey. Colors are mixed according to the fractions of trait-carrying species in each taxonomic group.

Calanidae show the fastest development rates through copepodite stages, with a median of 0.13 d^{-1} . Aside from Sulcanidae, Oncaeidae showed slow development rates, with 0.06 d^{-1} for *Oncaea mediterranea*.

3.11 Clutch size

Clutch size is below 35 for all taxa assessed, except for *Heterorhabdus norvegicus* from the family Heterorhabdidae, for which it is 94 (Fig. 6c). The lowest clutch sizes are found for *Scaphocalanus magnus* (Scolecitrichidae) and *Tharybis groenlandica* (Tharybidae), with 1.6 and 2, respectively.

3.12 Fecundity

Fecundity ranges from 113 for *Pseudodiaptomus pelagicus* to 2531 for *Sinocalanus tenellus* (Fig. 6d). The largest interquartile range of fecundity is observed for Centropagidae.

3.13 Spawning strategy

Free spawning is only reported for calanoid copepods (Fig. 7b). In most cases spawning strategy is assumed to be conserved within family, with the exception of Aetideidae, Arietellidae, Augaptilidae, and Clausocalanidae. Important free-spawning families are Acartiidae, Calanidae, Paracalanidae, Phaennidae, Pontellidae, and Scolecitrichidae.

3.14 Hibernation

We found literature reports on hibernation for 28 species, mostly belonging to the family Calanidae (Fig. 7c). Further families with hibernating species are Acartiidae, Clausocalanidae, Eucalanidae, Metridinidae, Pontellidae, Rhinocalanidae, Stephidae, and Subeucalanidae.

3.15 Resting eggs

The capacity to produce resting eggs has been observed for 47 species in total. Most of these species belong to the families Acartiidae and Pontellidae (Fig. 7d). Further families with resting-egg-producing species are Centropagidae, Sulcanidae, Temoridae, and Tortanidae.

4 Discussion

We collected information on more than a dozen functional traits of marine copepods and combined it into a structured database. Our work complements recent and ongoing efforts to develop zooplankton trait data collections. As for the collection of Benedetti et al. (2015), we focused on those traits of marine copepods that are the main determinants of fitness, also referred to as response traits (Violle et al., 2007). However, our collection covered the global ocean rather than the Mediterranean Sea and a different, though overlapping, set of traits. Hébert et al. (2016) recently published a trait

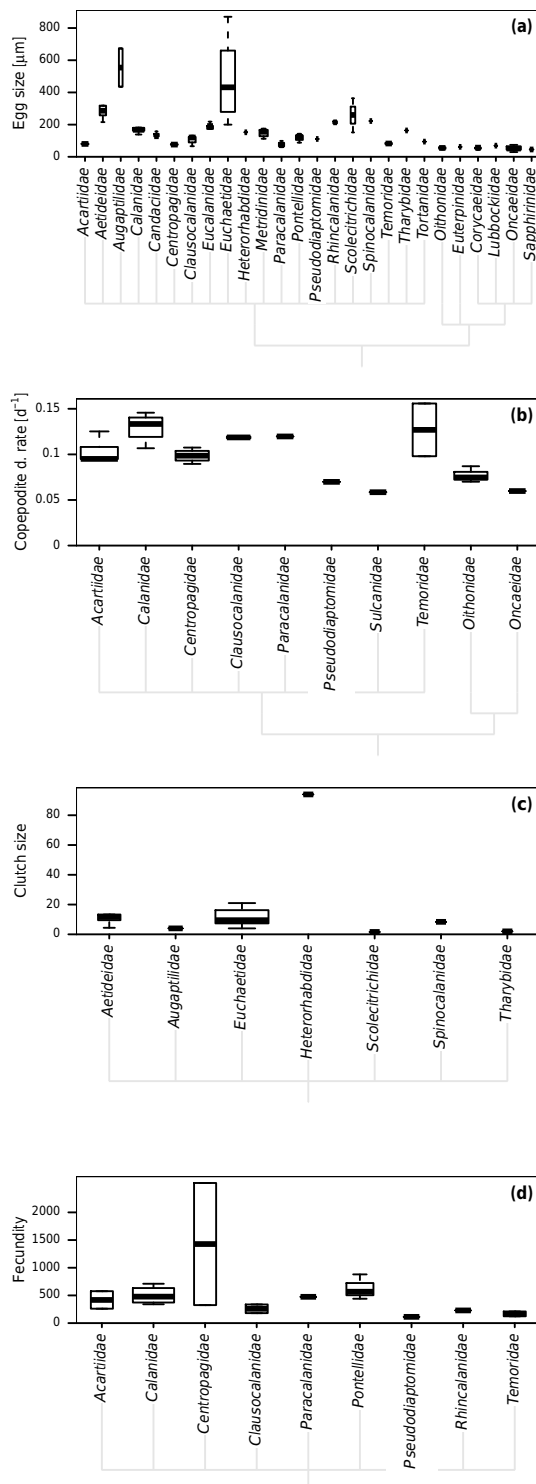


Figure 6. Reproductive traits grouped by family: family-wise box plots for egg diameter including converted values from μg carbon (a), development rate (b), clutch size (c), and fecundity (d). Thick lines on box plots illustrate median, boxes represent the interquartile ranges, and whiskers encompass the 95 % confidence intervals. Box plot width is proportional to the square root of sample size.

database on marine and freshwater crustacean zooplankton, which complementarily focuses on effect traits – traits which are expected to impact aquatic ecosystems. Aside from a few overlapping traits, this database mainly contains information about body composition and excretion rates. Another noteworthy, ongoing effort is the website maintained by Razouls et al. (2005–2016), who provide an impressive collection of information for around 2600 marine pelagic copepod species. While they focus on morphological descriptions, they also provide body length information, which in an aggregated way was also included in this database. In terms of taxonomic breadth and coverage of key functional traits as defined by the framework of Litchman et al. (2013) (Fig. 1), however, the data collection presented here is likely the most extensive to date. Nevertheless, our database has several limitations that should be considered.

4.1 Trait definitions

There are uncertainties regarding the definition of some traits and their associated trade-offs, in particular for hibernation and feeding mode. While we treat hibernation as a discrete phenomenon, in reality a host of hibernation forms exist, differing considerably in the degree to which metabolism is reduced (Ohman et al., 1998). Similarly, there are several feeding-mode classifications in the literature. We defined feeding modes after (Kjørboe, 2011), using trade-offs in feeding efficiency and predation risk as classification criteria. We note that the separation between cruise and feeding-current feeding is gradual and that many species are intermediate between these two categories. This is why we collectively categorize these feeding modes as active, which is distinctly different from passive ambush feeding.

Other classification schemes differ in particular with respect to ambush feeding. We define ambush feeding as a passive sit-and-wait feeding mode that targets motile prey with raptorial prey capture, which applies primarily to Oithona and related taxa. Alternatively, ambush feeding is sometimes defined solely based on raptorial prey capture (e.g., Benedetti et al., 2015; Ohtsuka and Onbé, 1991), but raptorial prey capture can also be observed in cruise and feeding-current feeders. Feeding types are sometimes also classified based on diet, e.g., herbivorous, carnivorous, or omnivorous (Wirtz, 2012); however, diet is not a trait in itself but rather a function of the feeding traits.

4.2 Taxonomic clustering of traits

The assumption that traits are conserved within taxonomic branches may not always hold. A large part of the diversity of pelagic copepods has only briefly been described in the literature, and little is known about the biology (Razouls et al., 2005–2016). Deeming a whole family to carry a certain trait therefore often means extrapolating from a few well-known species to many rare species. While this may be rea-

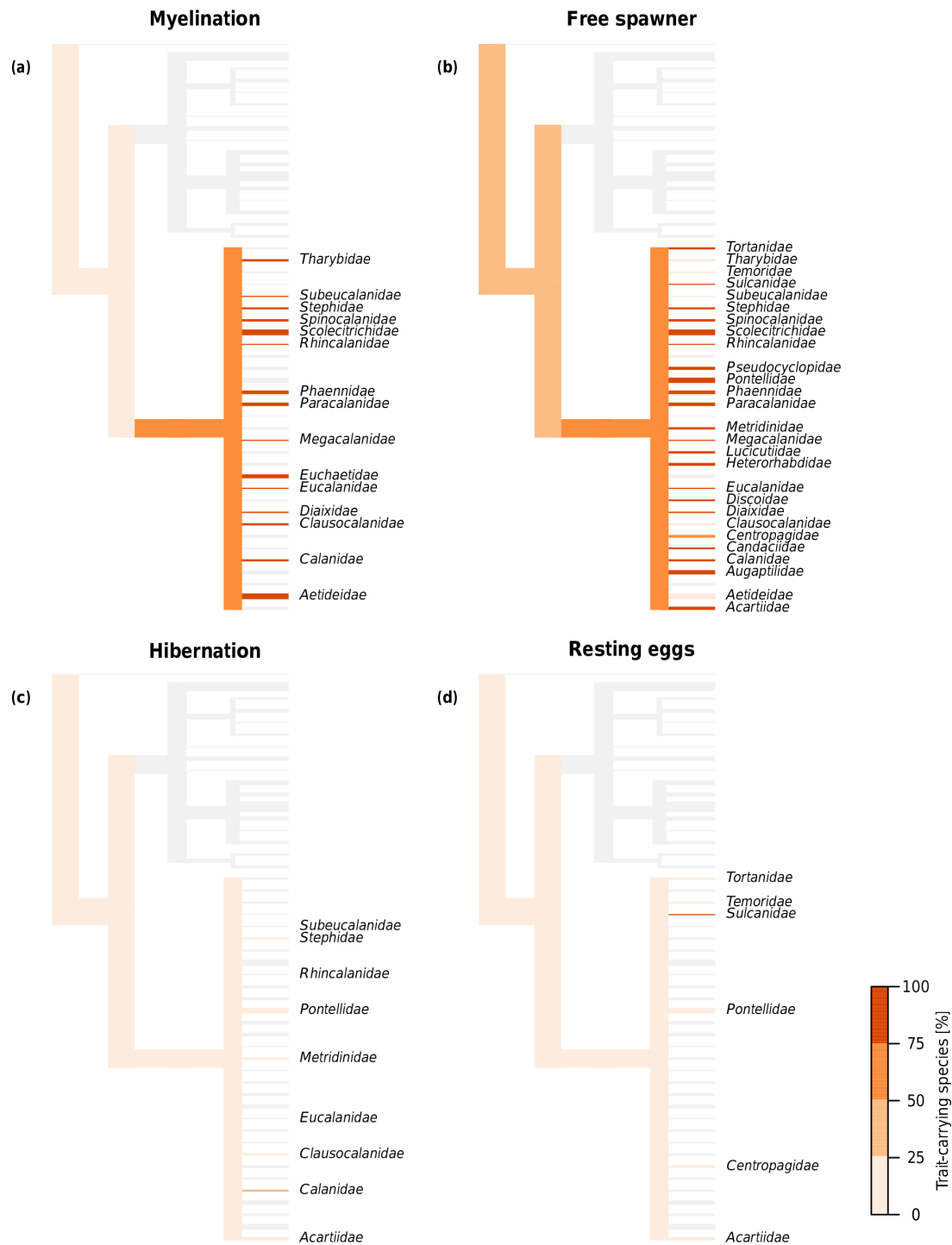


Figure 7. Taxonomic distribution of binary traits in the most important families of marine planktonic copepods. Fraction of trait-carrying species is illustrated down to the family level for myelination (a), spawning strategy (b), hibernation (c), and resting eggs (d). Families in which the trait is present in at least one species are labeled.

sonable for strongly conserved traits like myelination of the nervous system, for feeding mode and spawning strategy the appropriateness is less clear. Spawning strategy, for example, seems to be homogenous across most orders and fam-

ilies, yet in some calanoid families, such as Aetideae, both free spawners and sac spawners are found. Sometimes heterogeneity is observed even within genera: while the species *Euaugaptilus magnus* was found to carry its eggs, all other

observed species in that genus are free spawners (Mauchline, 1998). Our data on spawning strategy largely stem from Boxshall and Halsey (2004), who defined spawning strategy family-wise but noted in several cases that the assumption was not certain. We considered these remarks when we assigned a confidence level to the individual records.

4.3 Variance in quantitative traits

Quantitative traits are subject to measurement errors that may be significant, especially for traits that are difficult to measure or depend on parameter estimates, such as physiological rates (Kjørboe and Hirst, 2014). Where possible, we accounted for measurement errors by reporting standard deviations. However, in many cases this information was either not available or it was not retrievable with a feasible effort.

Furthermore, most important quantitative traits are strongly modulated by the environment (Kattge et al., 2011a). For example, we found a substantial intraspecific variation of adult body size in *Calanus finmarchicus* across the North Atlantic. Such variation is a consequence of genetic variation and phenotypic plasticity and may optimize fitness in response to biotic and abiotic environmental conditions. It may be interesting to study on its own; however, if not properly quantified, it introduces significant uncertainty in the data: point estimates from particular individuals and locations that happen to be in the data set may be an unrealistic representation of the species (Albert et al., 2010). We tried to account for this problem by including multiple trait measurements per species or averages over several measurements: however, for many species no more than one value could be found. The large investment required to measure copepod traits in the open ocean makes it difficult to overcome this limitation in the near future.

5 Data availability

The data can be downloaded from PANGAEA, doi:10.1594/PANGAEA.862968.

6 Conclusions

We produced a database on key functional traits of marine copepods that may currently be unique in their trait coverage and taxonomic breadth, enriching the field of trait-based zooplankton ecology. It may be used to obtain an overview over correlations between traits, to investigate the taxonomic and spatiotemporal patterns of trait distributions in copepods (e.g., Brun et al., 2016a), or to inform and validate trait-based marine ecosystem models. However, due to environmental modulation of many quantitative traits and the limited data availability, the database may not always provide robust estimates on the species level, making more detailed comparisons difficult.

A way to overcome these uncertainties in the future may be to establish a standard of “best practice” for the reporting of plankton trait data. Such data are most powerful in their raw form, when relationships between traits measured for the same individuals or groups of individuals are conserved. The handling of such data would be significantly facilitated if authors of observational studies published their raw data in table form, where measurements of different traits are reported together with relevant meta-information including location, time, environmental conditions, life stage, taxonomic classification, and measurement technique with its accuracy (Kattge et al., 2011a). Some scientists have already started to do so. For instance, Teuber et al. (2013) published an exemplary data set on copepod respiration. Flexible structures for trait databases, which are capable of storing such heterogeneous trait information, have been developed (Kattge et al., 2011a), and plant ecologists successfully implemented them in comprehensive efforts maintained by the scientific community (Kattge et al., 2011b). Learning from these experiences may lift the field of trait-based plankton ecology to the next level.

Appendix A: List of important pelagic families considered in figures

Acartiidae, Aetideidae, Arietellidae, Augaptilidae, Calanidae, Candaciidae, Centropagidae, Clausocalanidae, Diaixidae, Discoidae, Eucalanidae, Euchaetidae, Heterorhabdidae, Lucicutiidae, Megacalanidae, Metridinidae, Nullosetigeridae, Paracalanidae, Phaennidae, Pontellidae, Pseudodiaptomidae, Rhincalanidae, Scolecitrichidae, Spinocalanidae, Stephidae, Subeucalanidae, Sulcanidae, Temoridae, Tharybidae, Tortanidae, Cyclopinidae, Oithonidae, Monstrillidae, Corycaeidae, Lubbockiidae, Oncaeidae, Sapphirinidae, Aegisthidae, Euterpinidae, Harpacticidae, Miraciidae, Tisbidae, Misophriidae, Monstrillidae, Mormonillidae, Caligidae, Pseudocyclopidae, Peltidiidae, and Platycopiidae.

Competing interests. The authors declare that they have no conflict of interest.

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